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STUDIES ON SPIROSTREPTOID MILLIPEDS. XX. THE TAXONOMIC STATUS OF THREE POORLY-KNOWN SPECIES OF *GYMNOSTREPTUS* FROM BRASIL AND PARAGUAY (SPIROSTREPTIDAE)

by Richard L. Hoffman

ABSTRACT

The type material of *Spirostreptus ventralis* Porat, 1876, is not conspecific with material later identified as *ventralis* by Porat (1889) and Brolemann (1902), the latter being here renamed *Gymnostreptus porati*, nom. nov. (type locality: Alto da Serra, Sao Paulo, Brasil). *Spirostreptus microps* Porat 1876, is shown to be a senior synonym of *Mardonius legationis* Attems, 1950, and the species referred to *Gymnostreptus*. *Spirostreptus bovei* Silvestri 1895, studied from new Paraguayan material, is likewise considered referable to *Gymnostreptus*, closely related to G. *olivaceus* Schubart 1944, for which comparative notes and drawings are also provided.

A large number of millipeds were described before the primary importance of male genitalia in classification was appreciated. Even though some of these descriptions were long and detailed, they were inadequate when genera and higher taxa became based mostly on gonopod structures, and the species they represented formed a gigantic residue of *nomina dubia* with decades of nomenclatorial priority over later proposed and well-documented names. Obviously a high priority has been attached to the restudy of such species whenever original types, or reliable topotypic specimens, became available. The present paper is concerned with a still further reduction of the backlog of enigmatic Neotropical species in the family Spirostreptidae. The three species involved have a number of features in common, particularly the simple form of the gonopod telopodite and broad prefemoral lobe of the 1st legs of males, that suggest their inclusion in the genus *Gymnostreptus*, as somewhat inclusively defined by me in 1975. The internal diversity of this "Gymnostreptus" suggests however that more refined analysis of character systems may result in its rendition into a number of distinct generic groups.

I have to thank Dr. Jürgen Gruber (Naturhistorisches Museum, Vienna), Dr. Leon Baert (Institut Royal des Sciences Naturelles, Brussels), and Dr. E. Sylven (Naturhistoriska Riksmuseet, Stockholm) for access to material in museum collections under their care, and to Mr. John A. Kochalka for placing extensive material from Paraguay into my hands for study. Lastly, Dr. Henrik Enghoff (Zoologisk Museum, Copenhagen) provided fruitful and much appreciated manuscript review.

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Gymnostreptus

Gymnostreptus Brolemann, 1902, Rev. Mus. Paulista, 5: 153 (as subgenus of *Spirostreptus*). Proposed with four species, three of them new. Type species: *S.* (*G.*) *perfidus* Brolemann, by subsequent designation of Pocock, 1909.
Gymnostreptus: Hoffman, 1975, Pap. Avuls. Zool. S. Paulo, 28: 249. — Krabbe, 1982, Abh. Natur. Vereins Hamburg, NF 24: 319.

Gymnostreptus microps (von Porat), new combination
Figures 1, 2

Spirostreptus microps von Porat, 1876, Bih. K. sv. Vet.-Akad. Handl. 4 (7): 41. Two syntypes (Naturh. Mus. Stockholm) from "Corcovado" and "Pernambuco."
Spirostreptus microps: von Porat, 1889, Ann. Soc. ent. Belgique, 32: 226.
Spirostreptus microps: Brolemann, 1909, Cat. Fauna Brasileira, 2: 51.
Mardonius legationis Attems, 1950, Ann. Naturh. Mus. Wien, 57: 214, figs. 36-38. Male holotype (Naturh. Mus. Wien) from Rio de Janeiro. New synonymy!
Caicarostreptus legationis: Schubart, 1958, Arq. Mus. Nac., 46: 246.
Caicarostreptus legationis: Demange, 1970, Bull. Inst. fondt. Afr. noire, 32(A): 404.
Gymnostreptus legationis: Krabbe, 1982, Abh. Naturw. Ver. Hamburg, NF, 24: 319.

The name *microps* was based on a male and female from two localities in Brasil, and although the description was precise and good for its time, there was no reference to gonopod structure nor were these appendages illustrated. Porat again reported the species from Brasil (without exact locality) in 1889, and although his redescription did mention gonopod form it was hardly adequate to give a sensible impression.

In 1983 I studied both of Porat's samples as well as the type specimen of *Mardonius legationis* and can assert that all are conspecific. The following details about this material will be of interest.

Porat's original description mentioned a male and female specimen, and the two localities Pernambuco and Corcovado, but did not state which animal came from which locality. At present, the Naturhistoriska Riksmuseet contains two samples, one a male labeled "Brasilia, Kinberg 1852" and a female "Pernambuco, Forsell, 1847." I here designate the male as lectotype (it is so labeled) and presume it represents the Corcovado record although there is no specific label to that effect. Whether the female from Pernambuco is strictly conspecific I cannot say although the distance between the two places argues to the contrary.

A male in the Institut Royal des Sciences Naturelles, Bruxelles, is labeled "Brasilia, Van Volxem" and was correctly identified as *S. microps* by Porat. The gonopods of this specimen (Fig. 1) match those of the lectotype very closely; regrettably there is no precise locality information. Camille van Volxem is known to have collected around Rio as well as in the Serra dos Orgaos.

The male holotype of *Mardonius legationis* was collected at Rio by someone attached to the Austrian Embassy. The gonopods of this specimen (Fig. 2) match those of the *microps* lectotype precisely, and I herewith formally combine these two names as synonyms. In light of this association, it becomes almost certain that the lectotype was found on Mount Corcovado (a well-known Rio landmark) by Kinberg.

In preparing my 1975 paper on *Gymnostreptus*, I overlooked the obvious affinities of *legationis* and so did not take that name into account. Dr. Krabbe was quite correct to include *legationis* in her concept of *Gymnostreptus*, which was based upon the rather inclusive diagnosis that I proposed.

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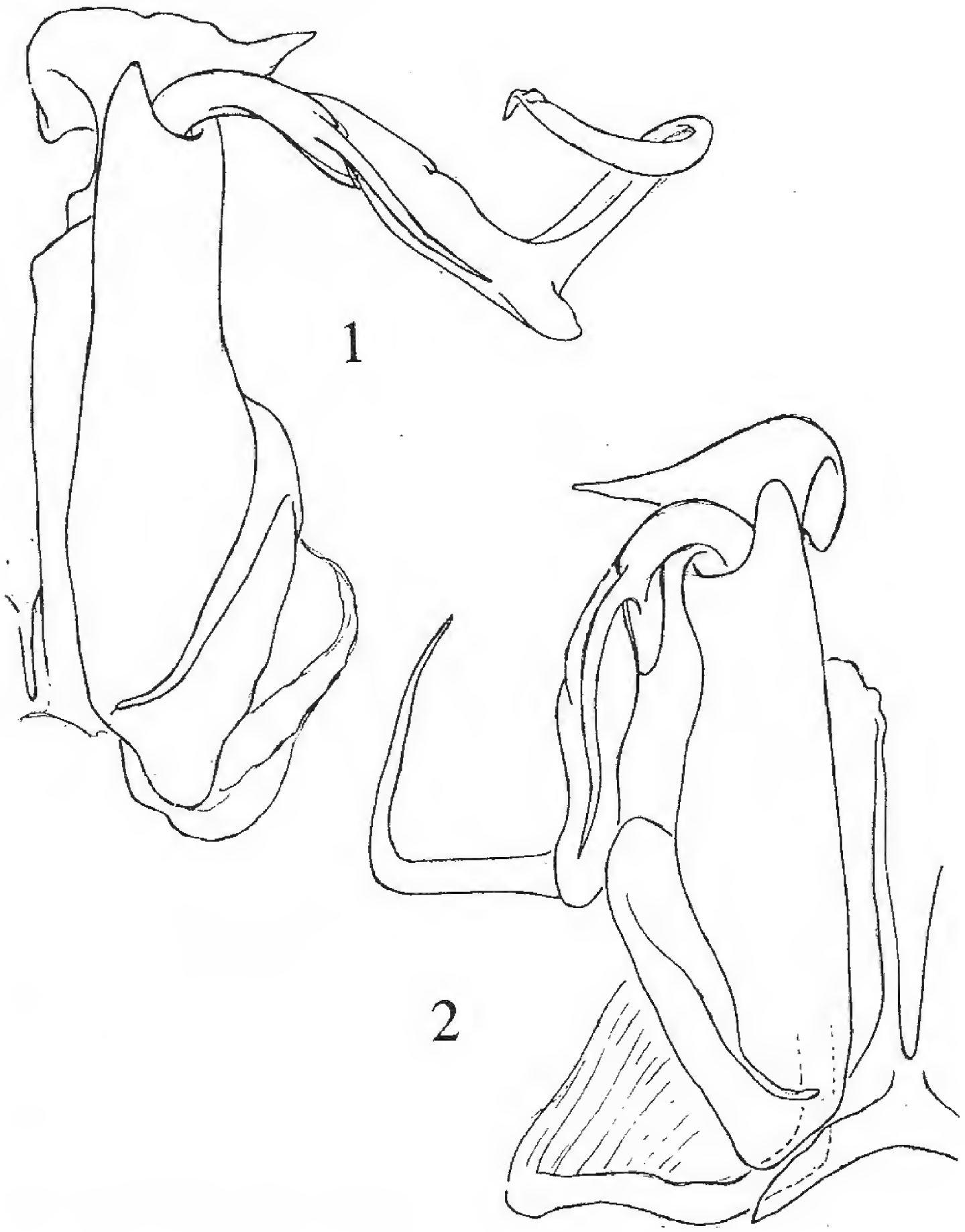

Fig. 1. *Gymnostreptus microps* (von Porat), right gonopod of specimen labeled "Brasilia" in IRSN. Fig. 2. The same, left gonopod of lectotype of *Mardonius legationis* Attems.

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With which of the seven species-groups defined by me does *microps* show any relationship? Each group was based on the structure of the gonotelopodite: presence or absence of a femoral process, expansion of the postfemur or none, and therefore, somewhat arbitrary. The closest match is perhaps with Group V (small spiniform femoral process and postfemoral region broadened with a moderate lateral lobe), especially with G. *bahianus* (Schubart).

Gymnostreptus ventralis (von Porat)
Figures 3, 4

Spirostreptus ventralis von Porat, 1876, Bih. svensk. Vetensk. Akad. Handl. 4(7): 42. Male holotype (Naturh. Riksm. Stockholm), said to have come from St. Thomas in the West Indies. [all of the many references to "S. *ventralis* Porat" published after 1902 (as well as Porat's own usage of the name in 1889) refer to the species so identified by Brolemann and should be associated with G. *porati*, described below].

Already in my 1975 paper I expressed doubt that the name *ventralis* as used by Brolemann in 1902 applied to the species originally described by von Porat, and a few years later was able to investigate the matter during visits to the collections at Brussels and Stockholm in 1983. As shown by study of the authentic male holotype of this species at Stockholm, while the species clearly belongs in *Gymnostreptus* as that genus is currently defined, it is clearly quite different from the species with which Brolemann associated *ventralis* in 1902. A brief summary of the case follows.

The original description was embedded in the format of a dichotomous key, and although fairly accurate in detail, did not allude to the male genitalia. Porat remarked that "Det beskrifna exemplaret är från Vestindien (S:t Thomas: Mus. Holm.)" and in the absence of evidence to the contrary the record was accepted by Pocock in his paper on Antillean millipeds (1894). However, in his report (1889) on juliform millipeds in the Brussels Museum, Porat again treated *ventralis* on the basis of material taken at "Therezopolis [Edo. Rio de Janeiro], Brasilia" which agreed with the original description in external body structure.

In working up the millipeds in the old "Museu Paulista" collection, Brolemann borrowed the Brussels specimens to examine the gonopod structure (of which he provided good figures in his 1902 monograph), and found close concordance with the gonopods of specimens from south-eastern Sao Paulo. Aware of the geographic problem of a West Indian species occurring in southern Brasil, he remarked "Cette difference de provenance est étrange et pourrait inspirer des doubtes quant à l'identité des deux types de Porat." Correct in this case, as he usually was, it is curious that Brolemann did not consult the actual type material in Stockholm. It is known that loans of types were made by that museum in the early 1900s, as many were sent to Portici for study by F. Silvestri, surely Brolemann would have been accorded the same courtesy.

Insofar as I can determine, all of the many references to the name "ventralis" made later than 1902 were based on Brolemann's identification, now considered to have been erroneous. As the species has apparently not acquired any junior synonyms during its lifetime, a new name must be provided for it.

Remaining is the unanswered question, what is the real homeland of the species *ventralis* sensu stricto? A small number of spirostreptids are known from several West Indian islands, but all are either endemic species of *Orthoporus* or obvious introductions of species (such as *Nanostreptus geayi*) native to South America. None have been collected at St. Thomas or elsewhere in the Virgin Islands. Either the material was mislabeled (a by no means rare event in museum history) or some other St. Thomas was implied by the label. The only attempt to consider either possibility known to me is the use of the Portuguese orthography "Sao Tomé" by Jeekel in his "Nomenclator" (1971: 129). Almost certainly the specimen came

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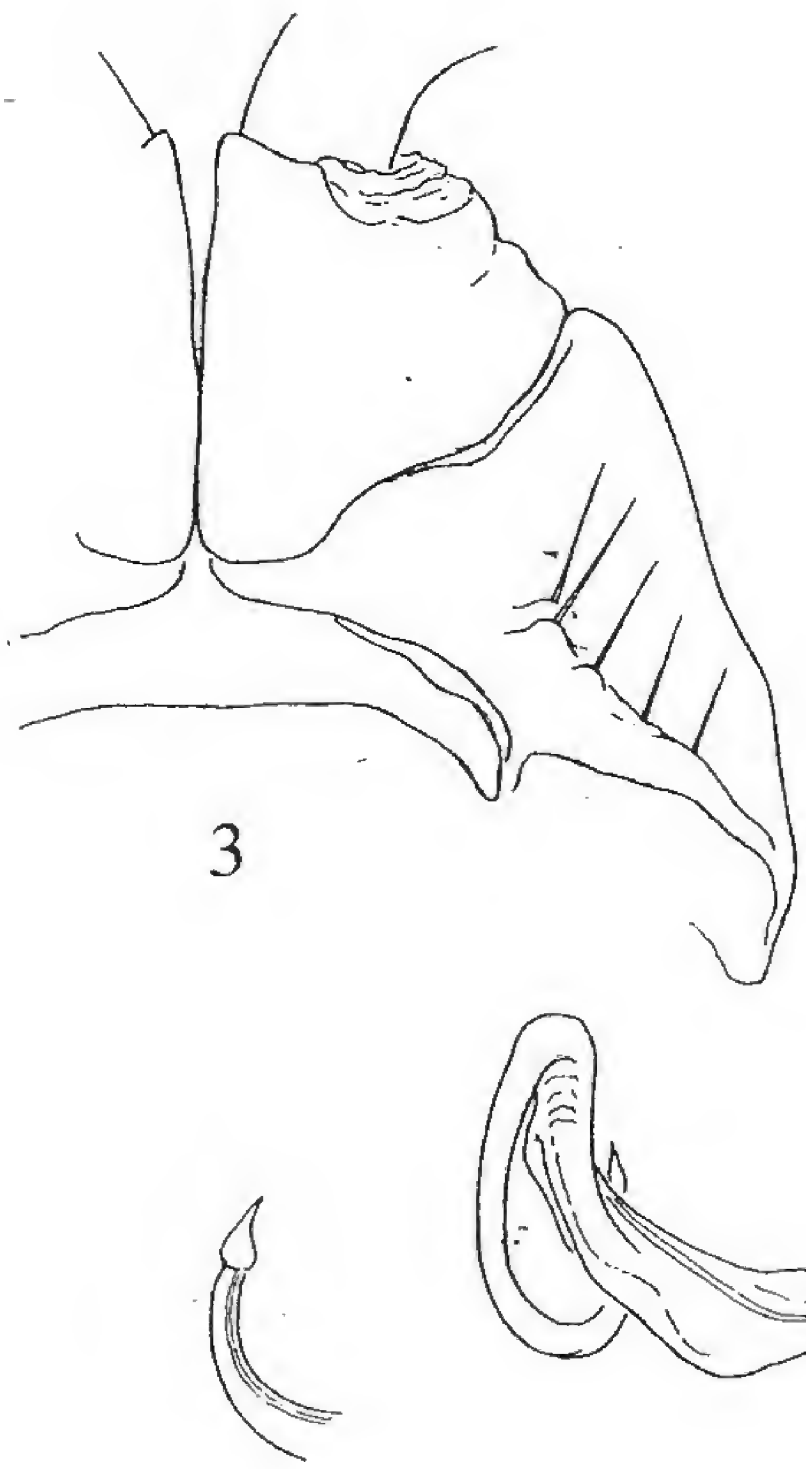
from Brasil, but specifically where? Thomas was apparently not a popular saint and few Brasilian places carry his name. The most plausible might be located about 100 km inland from Natal, Edo. RGN. The coastal town in northeastern Rio de Janeiro near Cabo Sao Tomé was more accessible to passing naturalists aboard ships, but does not seem to be in a biotope suitable for spirostreptids.



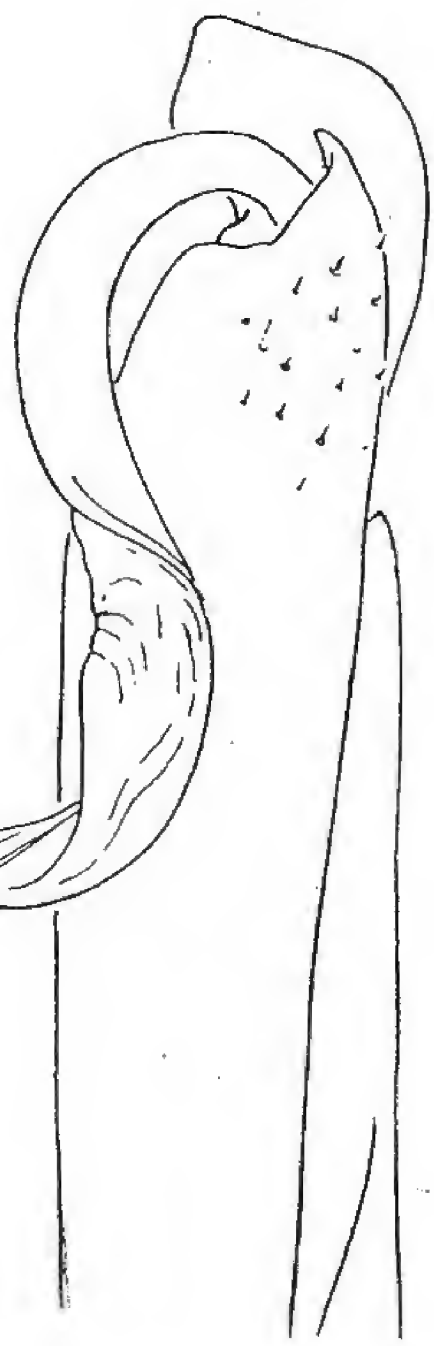


Fig. 3. *Gymnostreptus ventralis* (von Porat), coxosternal region of 1st pair of legs of male, oral aspect. Fig. 4. The same, distal half of left gonopod (both drawings from holotype).

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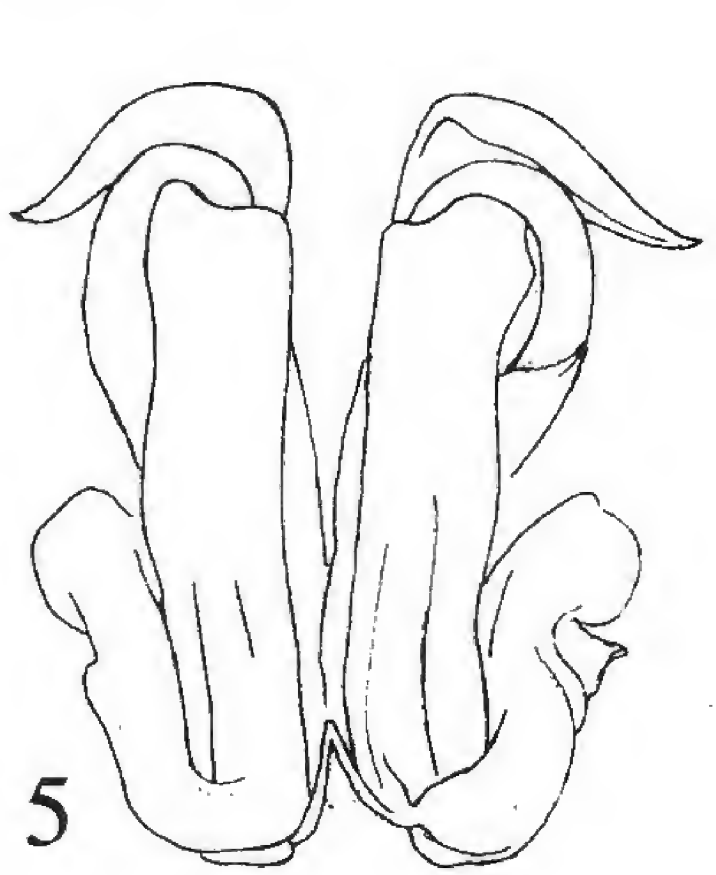
Gymnostreptus porati, new species
Figures 5, 6

Spirostreptus ventralis von Porat, 1889, Ann. Soc. ent. Belgique, 32: 228 (*nec Spirostreptus ventralis* Porat 1876) (specimens from "Therezopolis" Brasil).
Spirostreptus (Gymnostreptus) ventralis: Brolemann, 1902, Rev. Mus. Paulista, 5: 157, figs. 186-190. (Material from Alto da Serra [= Paranapiacaba], Sao Paulo, Brasil).
Gymnostreptus (Kochliogonus) ventralis: Verhoeff, 1941, Arch. Naturg. NF, 10: 296.
Gymnostreptus (Cochliogonus) ventralis: Verhoeff, 1943, Arq. Mus. Nac. 37: 255.
Cochliogonus ventralis: Schubart, 1945, An. Acad. Brasil. Cienc., 17: 82.
Kochliogonus ventralis: Attems, 1950, Ann. naturh. Mus. Wien, 57: 246.
Gymnostreptus ventralis: Hoffman, 1975, Pap. Avuls. Zool. Sao Paulo, 28: 250.
Gymnostreptus (?) ventralis: Krabbe, 1982, Abh. Naturw. Ver. Hamburg, NF 24: 327.

Despite the numerous references to this species (all cited by Krabbe [1982]), the only published drawings seem to be those of Brolemann (1902), reproduced here as Figures 5 and 6. He examined male specimens from Alto da Serra, Cerqueira Cesar, Os Perus, Piquette, and Cubatao, in addition to the material cited by Porat (1889) from Therezopolis, outlining an area extending southwest from the Serra dos Orgaos along the Serra da Mantiqueira to the vicinity of Sao Paulo.

Some of the above-mentioned specimens were returned to the Museu Paulista and are now in the collection of the Museu de Zoologia, Universidade de Sao Paulo. Others were retained by Broleman and after his demise went to the Museum national d'Histoire naturelle in Paris. In the interests of historical continuity, I designate the male from "Alto da Serra" as lectotype of *Gymnostreptus porati*; other specimens listed from Piquette, Os Perus, and Cerqueira Cesar can be considered as lectoparatypic.



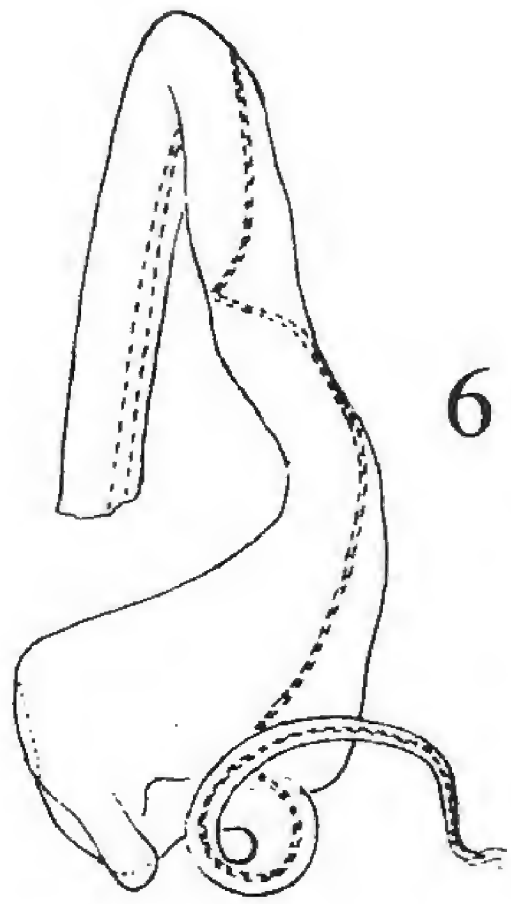


Fig. 5. *Gymnostreptus porati* new species, gonopods, oral aspect. Fig. 6, the same, telopodite, showing subapical clavate enlargement (both drawings adapted from Brolemann, 1902).

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Gymnostreptus bovei (Silvestri), new combination
Figures 7-14.

Archispirostreptus Bovei Silvestri, 1895, Boll. Mus. Stor. nat. Genova, (2) 12: 778, fig. 12. Syntypes, Mus. Civ. Stor. Nat. Genova and Lab. Ent. Agr. Portici, from Candelaria and San Ignazio [=Ignacio], Misiones, Argentina; G. Bove leg.
Spirostreptus bovei: Attems, 1914, Zoologica 25(65/66): 174. - Krabbe, 1982, Abh. Naturw. Ver. Hamburg, 24: 442 (in both references as *nomen dubium*).

Paraguayan material sent for identification by J. A. Kochalka includes a spirostreptid which agrees so closely with Silvestri's original account that specific identity seems assured. Moreover, the specimen was taken at a locality near those from which *bovei* was described. The collection data are (transcription from original label): "PARAGUAY: Dpto Itapúa: km 418 en Ruta 6. 12.XII.1983, abajo de tronco podrido, en una plantacion de tum. Colr. N. Scott."

Redescription: Adult male, ca 72 mm in length (fragmented); 6.2 mm in maximum diameter, body with 50 segments + epiproct. Coloration lost through preservation, but retaining narrow dark margin on the metazona as noted in the original description ("Color lurido-rufus, parte postica segmentorum nigra, antennis pedibusque sanguineis").

Head of typical form, smooth and polished; ocellaria relatively small (1.4 mm) and widely separated (IOD = 2.6 mm), ocelli in seven rows (11, 11, 10, 9, 8, 5, 3 = 57), those in the dorsalmost row much the largest, becoming smaller ventrad, those in the three shortest rows irregular and indistinct and easily overlooked. Gnathochilarium without special modification, prebasilar sclerite relatively broad transversely (Fig. 7). Collum narrowed ventrad with appearance of curvature posteriad, two well-defined oblique grooves and an indistinct short marginal groove (Fig. 8); Body segments generally smooth, prozona with five or six fine transverse striae, meso- and metazona densely micropunctate; metazonal striae very fine and horizontal below level of ozopores, becoming larger, sharper, and more oblique toward leg bases. Sterna with 10-12 transverse striae. Ventral ends of pleura in contact behind posterior coxae, forming closed coxal sockets. Legs (Fig. 9) relatively long and slender, postfemora and tibiae with prominent ventral pads except first and last five pairs; coxae of posterior pair of each segment slightly larger than anterior, subconically produced posteriad. Paraprocts moderately convex, thickened edges not set off by distinct depression.

Coxae of lst pair of legs (Fig. 10) with a distinct narrow belt of setae along contact with prefemora; basal prefemoral lobes moderate in size, acuminate, turned slightly laterad. Gonopods (Figs. 11-15) with elongated telocoxites, apex of posterior fold produced laterad into long acuminate process. "Paracoxite" notably elongated distad beyond its connection to posterior sternal sclerite (= *bride trachienne*; *ampoule*), broadened basally and closely applied to posterior base of coxal fold; no prominent glandular presence inside these two elements and no membranous modification of surface. Telopodite simple, unbranched, a small acute spine from end of femur at torsion, anterior surface beyond torsion unsclerotized, broadly white and membranous.

Gymnostreptus olivaceus Schubart
Figures 15-17

Gymnostreptus olivaceus Schubart, 1944, Acta Zool. Lilloana, 2: 402, figs. 67, 68. Male holotype (Mus. Zool. Univ. Sao Paulo), from Pirassununga, Edo Sao Paulo, Brasil.
Gymnostreptus olivaceus: Demange, 1967, Mem. Mus. Hist. Nat. Paris NS (A) 44: 93, fig. 90.

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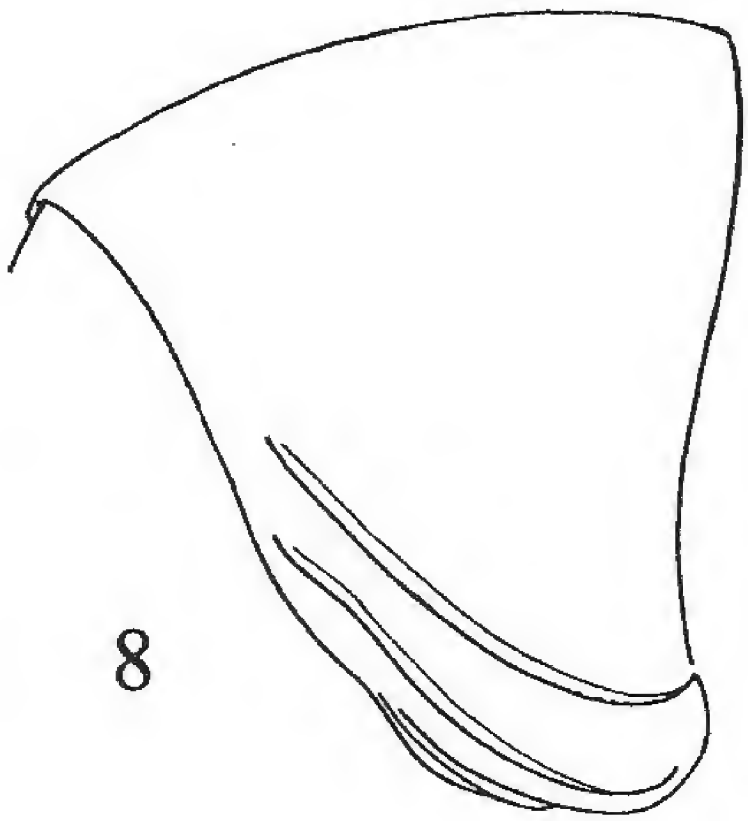

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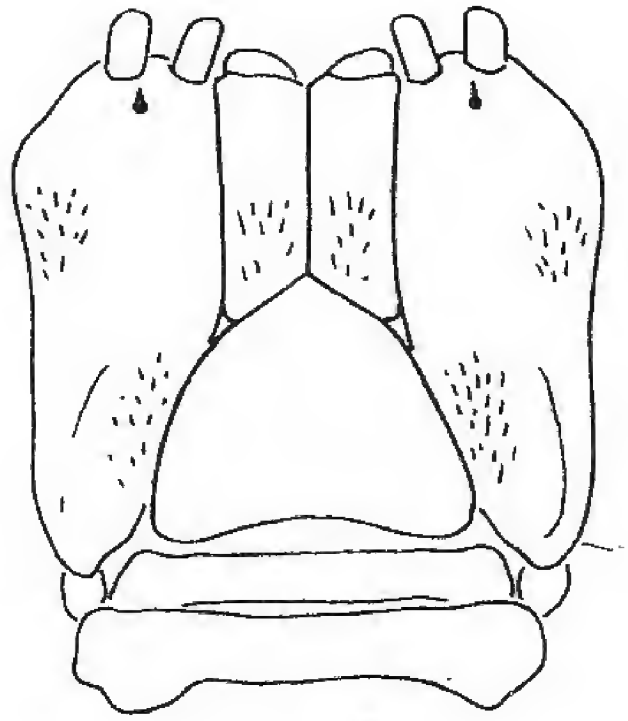

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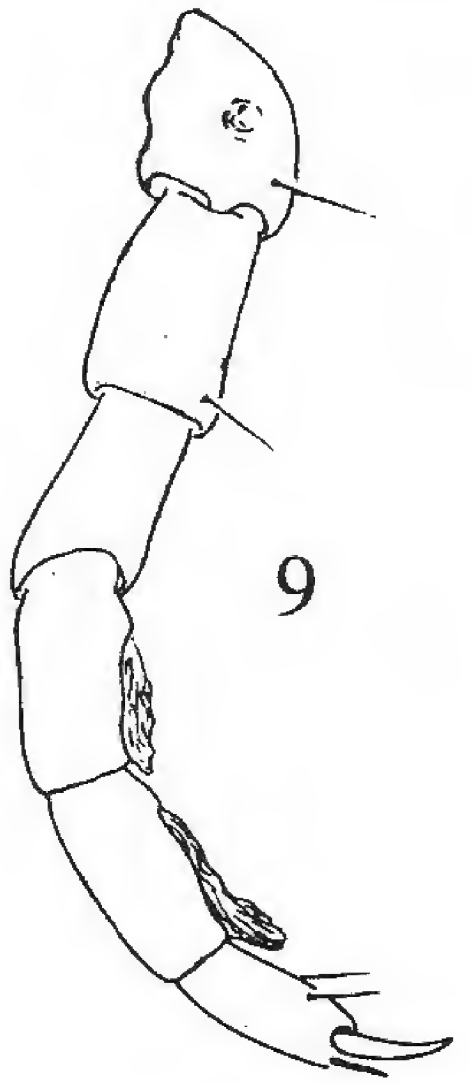

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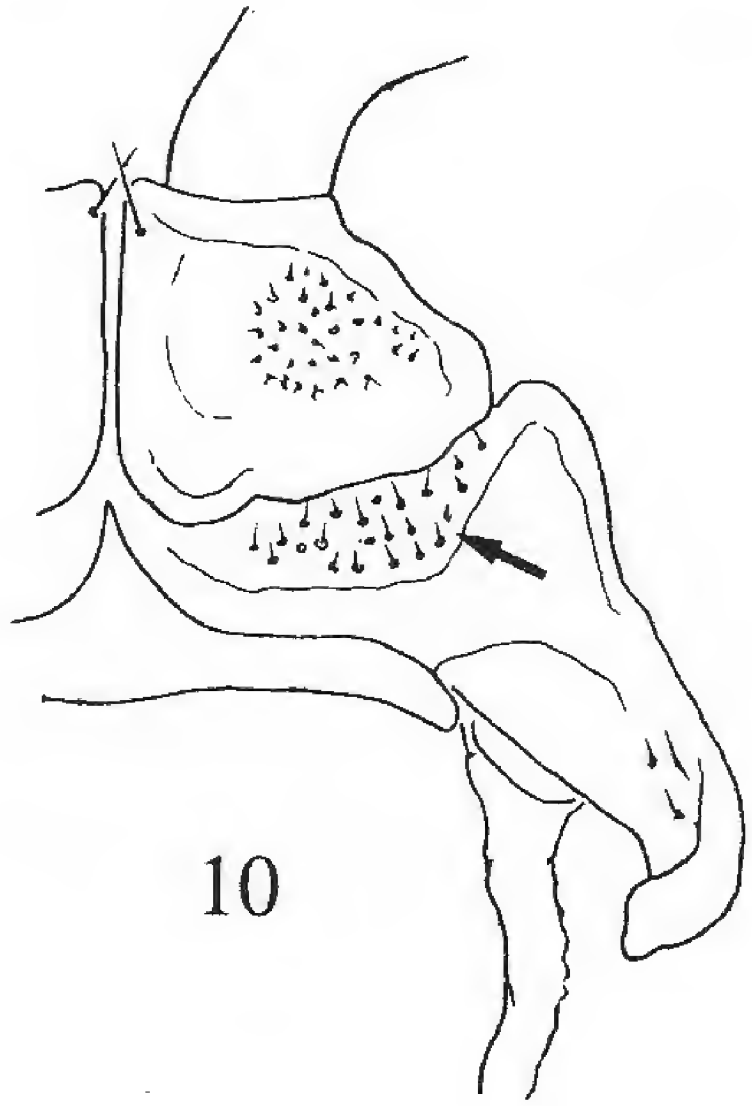

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Fig. 7. *Gymnostreptus bovei* (Silvestri), gnathochilarium. Fig. 8. Collum of male, left side. Fig. 9. Midbody leg. Fig. 10. Coxosternal region of first pair of male legs, oral aspect, arrow indicates field of small setae occurring also in several related species (see text).

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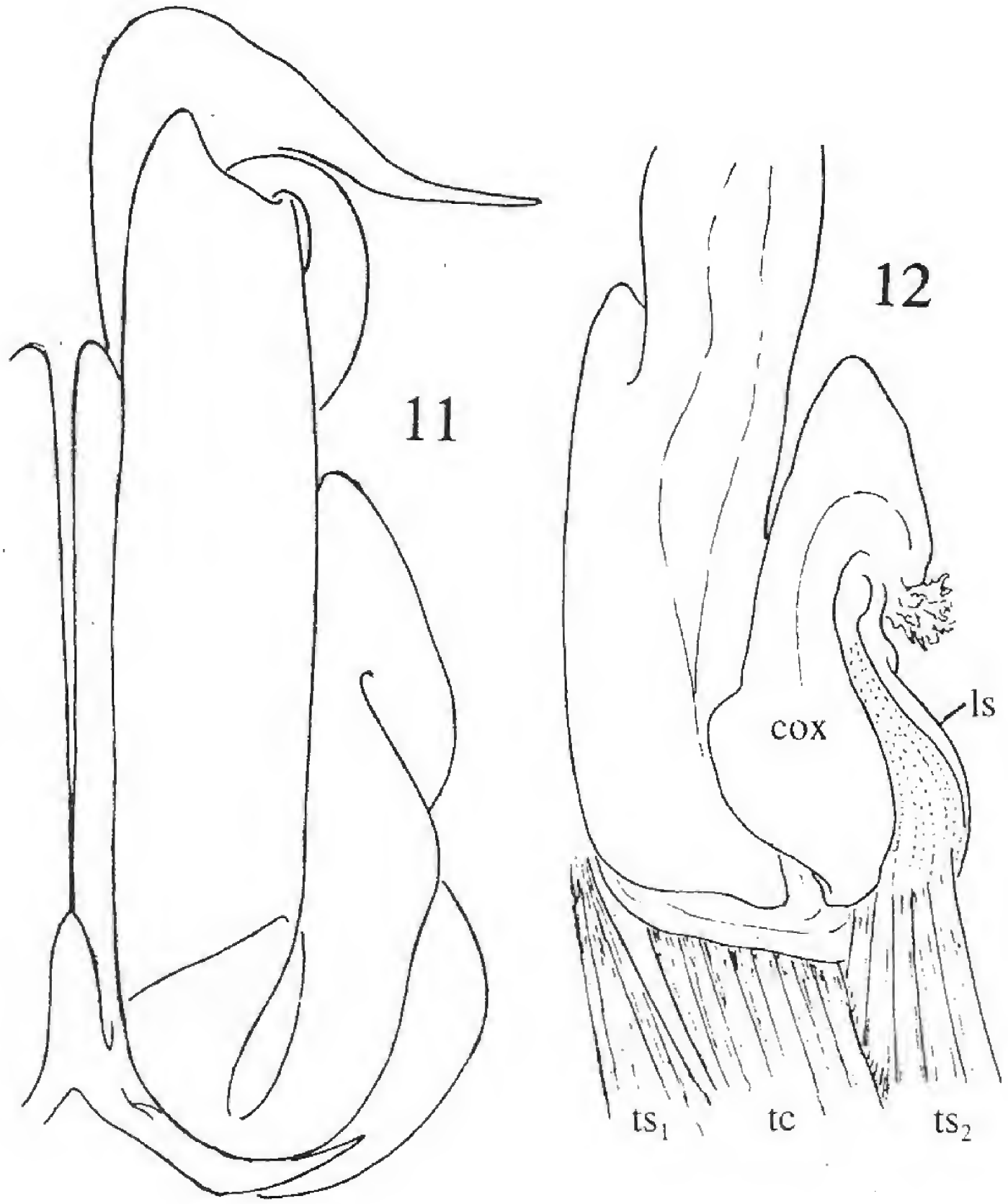

Fig. 11. *Gymnostreptus bovei*, right gonopod, oral aspect. Fig. 12. right gonopod, aboral aspect of base of coxal fold to show mesal placement of coxite (cox) and attachment of tracheosternal (ts) and tracheocoxal (tc) muscles.

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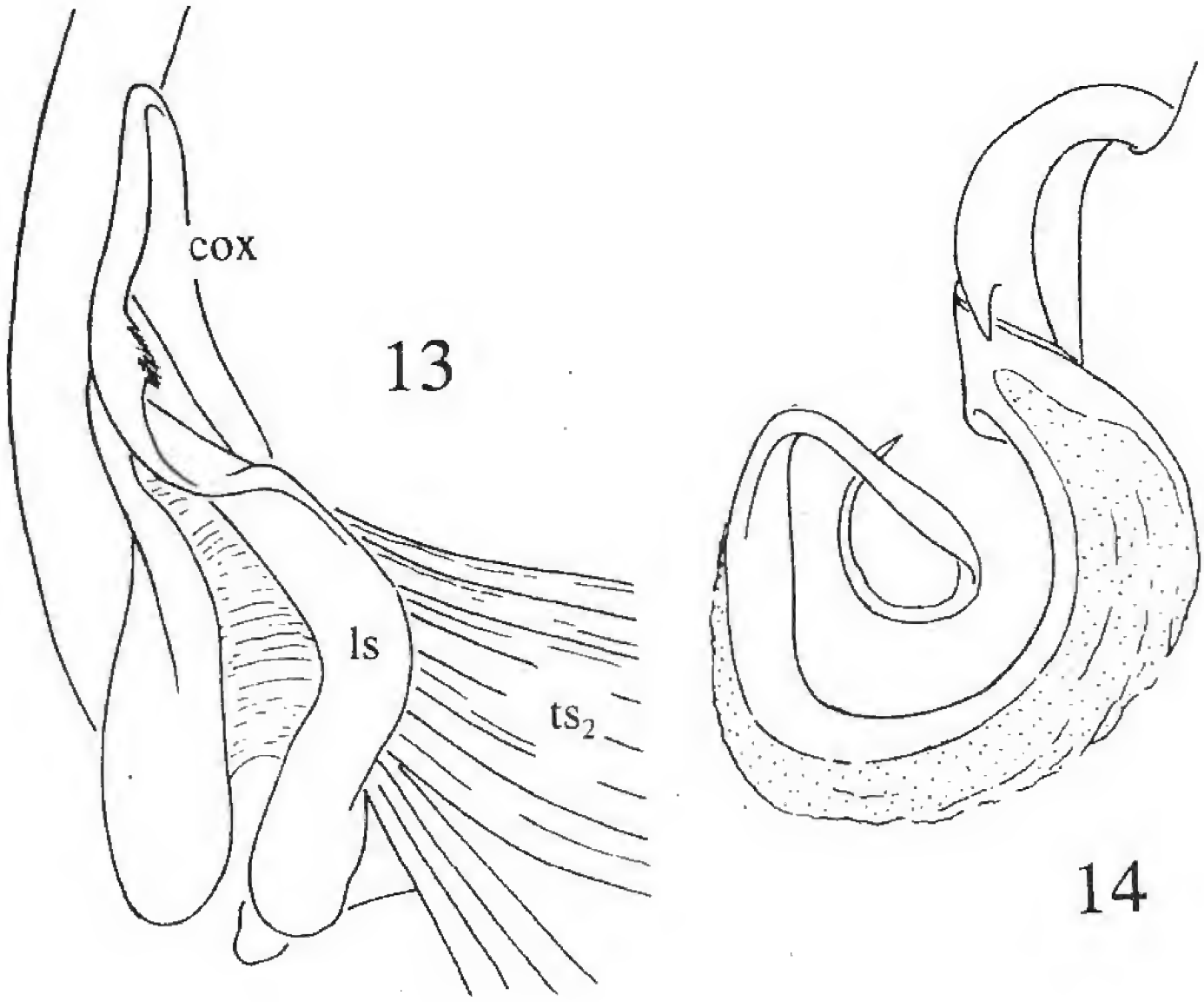

Fig. 13. *Gymnostreptus bovei*, base of left gonopod, lateral aspect, showing form of coxite (cox), posterior sternal element (ls), and tracheosternal muscles (ts). Fig. 14. Distal (exerted) part of telopodite, displaced in front of coxal fold thus seen in anterior aspect, stippled area denotes extent of white, membranous surface.

Material: Brasil: Edo. Sao Paulo, Mun. Anhembi, Ant. Remédios, February 1963, Werner Bokermann leg. (VMNH 4); Mun. Rio Claro, Rio Claro, December 1983, Alejo Mesa leg. (VMNH 3).

In general body size, segment number, and form of the first pair of male legs, there is a close agreement with G. *bovei*. While obviously members of the same species-group, these two taxa seem evidently distinct. There are notable differences in form of the collum (Figs. 8 and 15) and of the gonocoxal apex (much larger in *olivaceus*, cf. Figs. 11 and 17); the telopodite in *olivaceus* has a prominent subapical expansion while lacking the prominent white membranous area so conspicuous in *bovei*. An inconspicuous but constant character shared by these two and several others species of *Gymnostreptus* is a belt of small setae on the coxae of the first pair of male legs, adjacent and parallel to the proximal edge of the prefemur (indicated by arrow on the drawing for G. *bovei*, Fig. 10).

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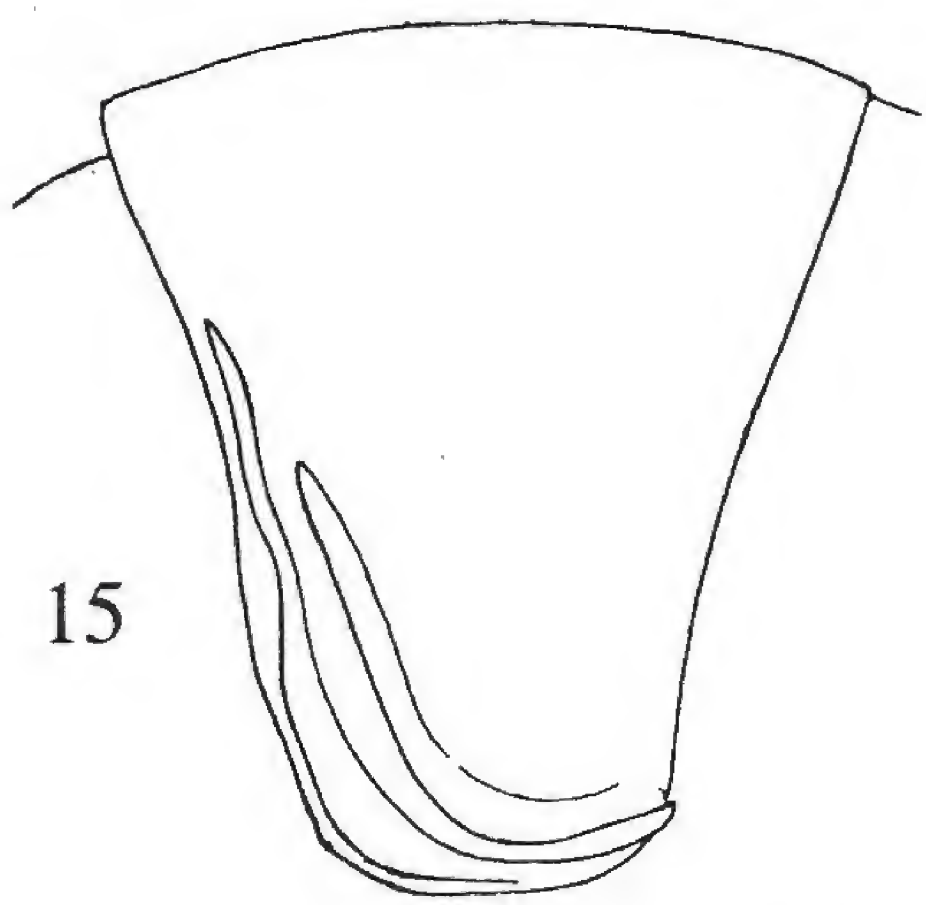

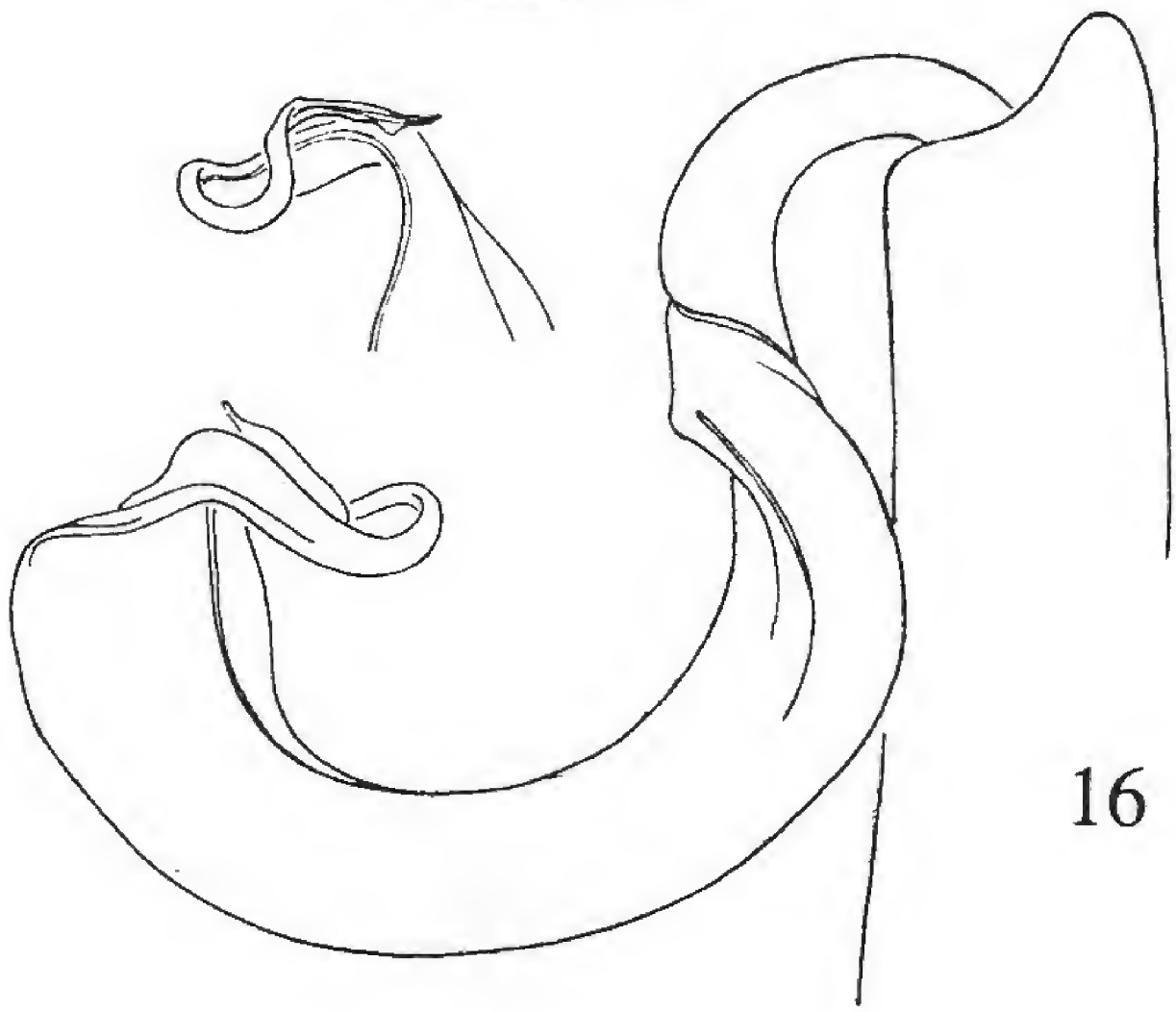

Fig. 15. *Gymnostreptus olivaceus* Schubart, lateral aspect of collum of male. Fig. 16. Distal (exserted) part of left telopodite, displaced anteriad in front of coxal fold, thus in anterior aspect (specimen from Rio Claro, Brasil).

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G. olivaceus appears to be widespread in the interior of Edo. Sao Paulo, thus vicariating with the more northeastern, coastal range of *porati*. It occurs on the west side of the Parana River at Porto Primavera, Mato Grosso do Sul (Schubart, 1958), at which point separated from the range of *bovei* by about 500 km. Presumably it will be found also in northwestern Edo Parana.

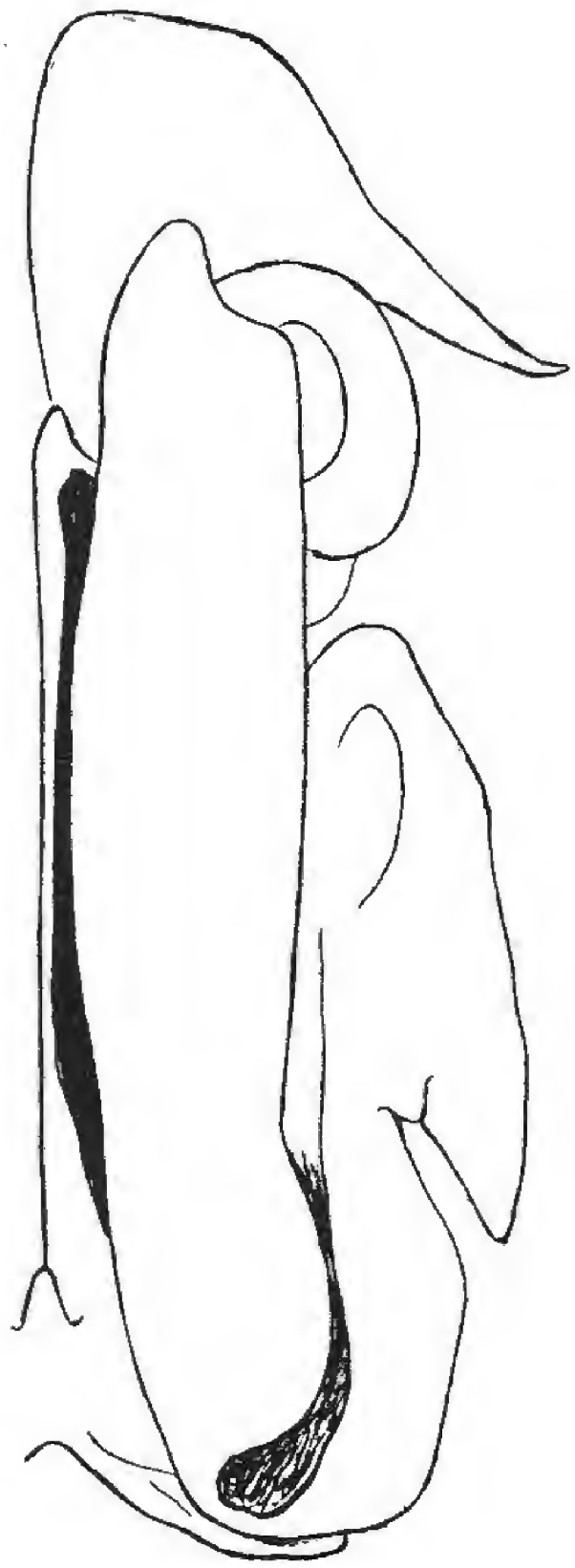

Fig. 17. *Gymnostreptus olivaceus*, right gonopod, anterior aspect (specimen from Rio Claro, Brasil).

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Commentary on gonopod structure

Because of the highly derived structure of the gonopods in spirostreptoid millipeds, in which the basal elements have become detached from the distal (telopodite), and the latter serves as a stabilized axis upon which the former move up and down during sperm transfer, interpretations of structural (and terminological) homologies have varied substantially during the past century.

The existing definitive treatment of gonopod structure is that of Demange (1967), who clearly described and illustrated both the sclerotized elements and their musculature. The factual material in his account is unimpeachable, but I believe that a somewhat different interpretation of anatomical identities can be derived from both Demange's information and my own experience with these animals.

Typically the paired spirostreptid gonopods consist of a small (or absent) median sternal element; two elongated distal elements ("telocoxites") each in the form of a folded structure that encloses the basal half of the telopodite; and a smaller unit on each side. Consensually, the structural identity of the large paramedian telocoxites has been considered morphologically homologous with the coxae of the walking legs. The smaller laterobasal structures have generally been termed "paracoxites". They consist of an inner and outer division joined by membrane, and are attached basally to the anterior (lateral) fold of the telocoxite by either extensive fusion, a flexible articulation, or a spectrum of intermediate conditions. Traditional taxonomic procedure has incorporated a nearly complete disregard of paracoxite structure and potential value in systematics.

As recently as thirty years ago (Kraus, 1966, fig. 16), the two divisions of the paracoxite were not distinguished anatomically, although it is clear from his (and many other) illustrations that the inner of the two is attached to the anterior coxal fold, while the outer is completely fused (not articulated) with the base of the telopodite. In the following year, Demange (1967: 91) clearly distinguished between "le paracoxite" and "le renflement "ampullaire de la base télopodiale" which he also termed the "ampoule" (*am* on his illustrations). His identification of muscles inserting on this "ampoule" as tracheocoxal (Fig. 90, tc.g.^{2,3}) reflect his opinion that the "ampoule" is of coxal origin.

In the material which I have examined, the so-called tracheocoxal muscles actually insert primarily on the posterior edge of the "ampoule", although there is a definite contingent of smaller muscles extending from the tracheal apodeme to the caudal base of the coxal folds and to the paracoxite (plus a still smaller muscle inserting on the median sternal element).

From the example of diplopod ambulatory legs considered to represent a generalized condition (e. g., platydesmoids and the first two pairs of legs in polydesmoids), it is evident that coxal sockets were - plesiomorphously - entirely enclosed by the sternum. This structure is logically present in gonopods as well, although the sternum becomes progressively reduced on the posterior side in most taxa. In spiroboloids, for instance, the gonosternum is nearly complete on the posterior side, except for a median interruption necessitated by the enclosure of the posterior gonopods within coxal cavities of the anterior pair. It is only logical that an anatomically comparable sternal remnant should occur even in spirostreptoids, and that this does occur in immature males is obvious from, e. g., the illustration given by Brolemann (1927: fig. 36) which shows that the sternum initially crosses the bases of the still-indeterminate coxae and telopodites to curve around behind the coxae. In millipeds generally, there appears to be a clear trend toward reduction of the median sternal element, and fusion of the lateral ends with the coxae (thus in polydesmidans, the "coxa" of the gonopods is actually the "coxosternum"). In spirostreptoids, the mechanical imperatives of gonopod function require fusion of the telopodite base with the lateral ends of the sternum (and the tracheal apodeme) rather than with the adjacent region of the coxa, and from Brolemann's cited figure, it is easy to see how this can be accomplished. I believe that a good

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case can be made for interpretation of the "ampoule" as actually the lateral end of the original sternum, fused at one end with the base of the telopodite, and with the paracoxite at the other. This interpretation, already implied in connection with the African genus *Microtrullius* (Hoffman & Howell, 1995: 184), removes much of the "special nature" of the spirostreptid gonopod and brings it into accord with the structure present in other juliform groups. If such a concept can be confirmed by further studies, one further consequence would be identification of the erstwhile "paracoxite" as the real anatomical coxa, with the elongated coxal folds thus secondary developments analogous - if not homologous - with "colpocoxites" that occur widely and diversity in the Chordeumatida. A second is that the telopodite + tracheal apodeme fusion produces the anatomical analog of the "cheirite" in chordeumatids.

It may be kept in mind that Jeekel (1985: 107) discussed a somewhat different interpretation of spirostreptid gonopods, namely that the paracoxites, lateral sternal elements, and basal region of the telocoxites correspond collectively to the original coxa, that the apical half of the telocoxite represent the original telopodite, and the telopodite is the equivalent of the pseudoflagellum present in some Australian cambaloid genera thought to be "ancestral." So far I have been unable to completely assimilate these possibilities into my own perceptions and refrain for entering into a discussion of their relevance.

Commentary on amphiatlantic spirostreptids

For a long time, up to just a few decades ago, many authorities believed that some spirostreptid genera were represented by species in both Africa and tropical America. A gradual departure from that position culminated in the monograph on Spirostreptidae by Dr. E. Krabbe (1982) in which no amphiatlantic genera whatever were recognized. In fact, in some cases the ocean itself appeared to be the only generic distinction, and it is true that there is still a long way to go in making anatomically-based separations between some of the presumably related vicariant taxa. A lot of African species have gonotelopodites that look like those typical of *Gymnostreptus*, for instance. An era of careful and detailed redescription and comparison of different character systems obviously needs to be inaugurated. Any arrangement constructed on a single system seems likely to be only illusory.

However, a major distinction between the two continental faunas might be brought to the attention of those interested in the classification of this family.

In the vast majority of African spirostreptids, sigilla are present on the inner surface of the metazona and the gonotelopodites are held - when at rest - on the anterior side of the gonopods. In the vast majority of Neotropical spirostreptids, sigilla are not present, and the gonotelopodites are normally recurved caudolaterad laterad to the posterior side of the gonopods. While there are exceptions to both these rules, the preponderance of cases is so pervasive and consistent as to suggest that these fundamental patterns were already in place prior to ?mid-Mesozoic development of the Atlantic Ocean.

Insofar as currently known, sigilla are present in the majority of African spirostreptid genera, and in the majority of Afro-Asian species of Harpagophoridae, reinforcing the already known relationship of these two families. I do not know of any occurrence in the Odontopygidae, or in any of the "satellite" spirostreptomorph taxa such as *Pseudonannolene*, *Choctella*, *Phallorthus*, or *Physiostreptus*. However, these structures have been recently reported (Enghoff, 1995) for a number of species in the genera *Paectophyllum*, *Macheiroiulus*, *Calyptophyllum*, and *Catamicrophyllum*, in the dominantly Palearctic family Julidae. Whether these widely disparate occurrences represent the expression of a latent (recessive) genotype present in the genome of some remote julid-spirostreptid ancestor, or an independent genetic re-invention of the trait *de novo* cannot be estimated at present. Nor is enough known about the relative evolutionary status of Old and New World spirostreptid taxa to categorize the

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presence of sigilla as a generalized or derived trait. Eventually this will become manifest with the development of an adequate classification.

It is difficult for me to comprehend vicariance and dispersal as two separate evolutionary mechanisms rather than two consecutive phases of a single ongoing process. In this case, ancestral spirostreptids simply must have widely dispersed from their point of origin somewhere in Gondwana to provide the far-flung taxa later separated by some vicariance events (origin of the Atlantic in this case).

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